PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(1):136–146. 1995.

A juvenile of the scaled squid, *Pholidoteuthis adami* Voss, 1956 (Cephalopoda: Oegopsida), from the Florida Keys

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Abstract.—I describe a heretofore unknown, small juvenile (54 mm mantle length) of *Pholidoteuthis adami,* a member of the uncommonly captured, systematically confused lepidoteuthid squids. I used scanning electron microscope photomicrographs to examine the dermal cushions and tentacular suckers, which are distinguishing features in the adult. I compared these features with larger specimens of 108 mm and 179 mm mantle length. The dermal cushions of the smallest specimen are conical, but in the larger specimens they are flatter, oblong in shape or roughly pentagonal, and closer together and often touching one another at the base. In all growth stages the dermal cushions are interiorly vacuolated. The tentacular suckers of the smallest specimen have oval openings. However, in the larger juveniles the tentacular suckers are laterally compressed and have narrow openings as in the adult. The structure of the dermal cushions of the juveniles and apparent developmental patterns suggest that a congeneric relationship with the type of the genus, *P. boschmai,* may not be valid.

The "scaled" squid *Pholidoteuthis adami* is a pelagic species that reaches 780 mm in mantle length (ML; Roper et al. 1969). Adult *P. adami* have two peculiar features: roughly pentagon-shaped dermal cushions on the mantle, and tentacular suckers that are laterally compressed and have narrow openings. This species occurs in shelf and slope waters throughout the Caribbean and Gulf of Mexico and adjacent northwest Atlantic Ocean and may have fisheries potential (Roper et al. 1984). However, *P. adami* was described only relatively recently by Voss (1956), and is infrequently collected, although it has been observed in large schools at night at the surface in the upper Gulf of Mexico. Additional accounts of *P. adami* in the literature are few: it has been reported from the northern Gulf of Mexico (Lipka 1975), off the eastern United States (Rathjen 1981), off Suriname and French Guiana (Okutani 1983), off Venezuela (Arocha et al. 1991), and observed on the Cape Hatteras slope in a submersible (Vecchione & Roper 1991). Additionally, 38 juvenile and adult specimens from the largely unreported collection of the Rosenstiel School of Marine and Atmospheric Science (RSMAS) Invertebrate Museum were mostly captured in shelf and slope waters in the upper Gulf of Mexico and off Columbia.

The genera *Pholidoteuthis, Lepidoteuthis,* and *Tetronychoteuthis* have been placed in the family Lepidoteuthidae because they all possess prominent, scale-like dermal structures on the mantle. However, the systematics of these taxa are confused. Their status was evaluated by Roper & Lu (1989), who recommended that *P. adami* be placed in the family Lepidoteuthidae based on the similar morphologies of the gladii and structure of the dermal cushions of *P. adami* and *Lepidoteuthis grimaldii.* However, Nesis & Nikitina (1990) revised the Lepidoteuthidae and concluded that *Pholidoteuthis* should be in a separate family, Pholidoteuthidae, and that the two nominal species of *Tetronychoteuthis, T. massyae* and *T. dussumieri,* are synonymous with *Pholidoteuthis boschmai. Pholidoteuthis boschmai* is found in the eastern Atlantic and southern Indian oceans and may not be congeneric with *P. adami* based on marked differences in the gladii (Toll 1982).

The dermal structures of these squid were described in detail by Roper & Lu (1990) and were designated as dermal cushions in *Pholidoteuthis adami* and *Lepidoteuthis grimaldii,* and papillose tubercles in *Tetronychoteuthis massyae* in recognition of their different morphologies. The structures of all three genera are composed of fibrous connective tissue and are extremely vacuolated. The dermal cushions of *P. adami,* and other vacuolated tissue in the mantle, may contain ammonium ions to aid in buoyancy. Additionally, Roper & Lu (1990) postulated that dermal cushions may aid these squid in reduction of hydrodynamic drag by controlling laminar flow in the boundary layer to reduce turbulence.

I describe here an exceptionally well-preserved, previously unknown, small juvenile *P. adami* from the Straits of Florida off the Florida Keys. Additionally, I utilize scanning electron microscopy (SEM) to characterize the dermal cushions and tentacular suckers of a size series of three juveniles in order to elucidate the development of these features, and to help understand the relationship of *P. adami* with other lepidoteuthids.

Materials and Methods

Seasonal zooplankton and physical oceanographic surveys were conducted off the Florida Keys from May 1989 to Jan 1991 by the Southeast Florida and Caribbean Recruitment project (SEFCAR; Lee et al. 1992). Discreet depth zooplankton samples from the surface to 200 m were collected with a Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS) with a 1 m^2 fishing mouth (Wiebe et al. 1976). I analyzed distribution of planktonic cephalopods from four SEFCAR cruises from Aug 1989 to May 1990 (Goldman & McGowan 1991, Goldman 1993). One juvenile *P. adami* of 54 mm ML and 104 mm total length was captured on 14 Feb 1990, 2035–2041 h GMT, during the R/V *Calanus* cruise CA9002, off the central Florida Keys at 24°31.93′N, 81°03.20′W. The depth of capture was between 78–101 m over a 200 m bottom depth. The specimen was fixed in a 10–15% formalin-seawater solution and subsequently transferred to 70% ethanol. It has been deposited in the RSMAS Invertebrate Museum (UMML 31.2636). I examined two additional specimens from the collections of that museum. These are larger juveniles of 108 mm ML (UMML 31.2369; R/V *Oregon* 4902, 28 May 1964) and 179 mm ML (UMML 31.465; R/V *Oregon* 3221, 4 Mar 1961).

I prepared specimens for SEM photomicrography in different ways. Samples from the museum specimens were dehydrated in ethanol, hardened with hexamethyldisilazane (HMDS) and dried in a desiccator for 24 h, then sputter coated them with palladium. These preparations resulted in severe shrinkage of the mantle tissue. The dermal cushions collapsed and were flat. However, the tentacular suckers, which contain hard chitin rings, were unaffected by shrinkage.

I re-hydrated and re-fixed a second group of samples from the same specimens in 2% glutaraldehyde for 1.5 h. After dehydration in ethanol, one set of tentacle and mantle samples was hardened with HMDS and another set was dried by critical point drying (CPD). The set of re-fixed samples treated with HMDS exhibited severe shrinkage. However, the samples dried by CPD produced dramatically improved results; dermal cushions looked spongy and were highly vacuolated. The latter technique was used on samples from the SEFCAR specimen.

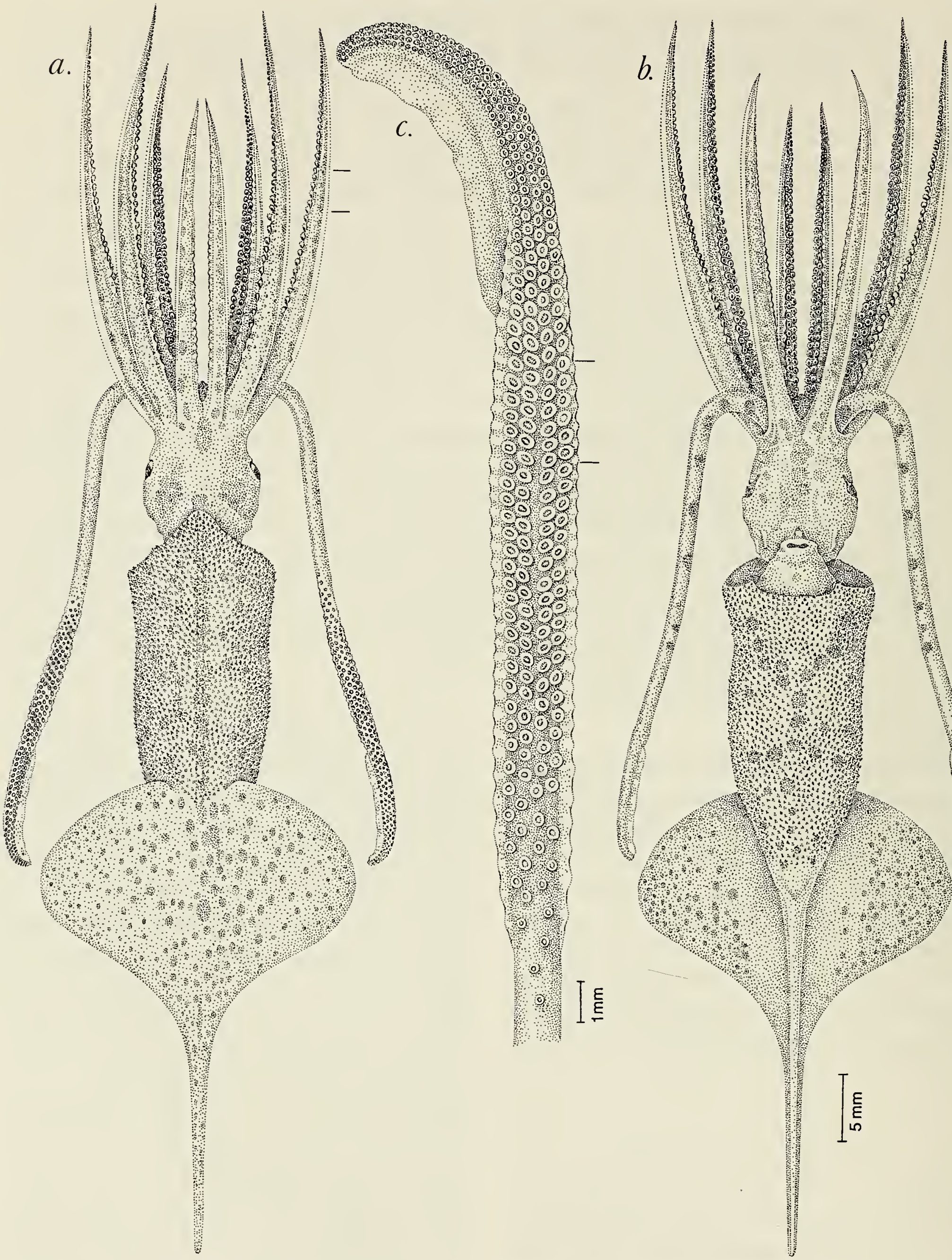

Fig. 1. Juvenile *Pholidoteuthis adami* from the Florida Keys, 54 mm ML, UMML 31.2636: (a) dorsal view, unlabeled bars indicate section illustrated in Fig. 2a, (b) ventral view, and (c) closeup of left tentacular club, unlabeled bars indicate section illustrated in Fig. 2c.

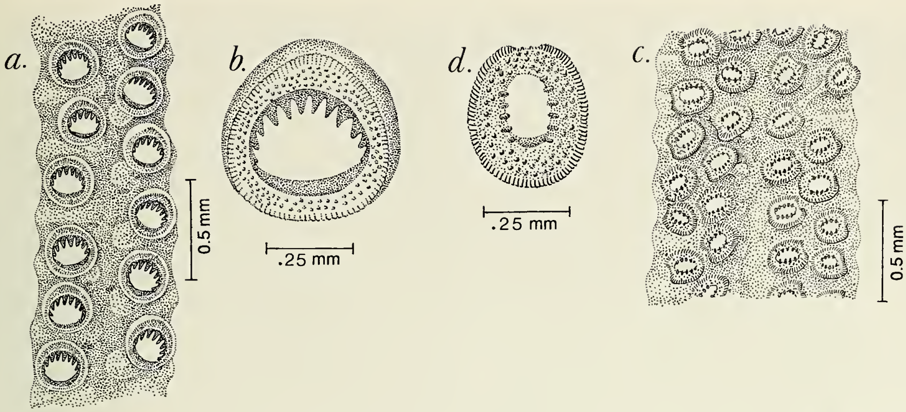

Fig. 2. Juvenile *P. adami,* 54 mm ML: (a) ventral view of middle section from right arm III, lowest sucker is 24th from base in dorsal row, (b) largest right arm III sucker, 18th from base in ventral row, (c) section from left club manus, and (d) sucker from left club manus.

Results

Description of 54.2 mm ML, female juvenile.—(Figs. 1–2).

Mantle: Walls firm. Thickness varies from about 0.3 to 0.4 mm. Constricted just posterior to the anterior mantle margin. Bulges in center where mantle width (MW) is maximum. Laterally compressed, presumably an artifact, so that MW is 8.7 mm (16.1% of ML) measured laterally, 12.7 mm (23.4% of ML) dorso-ventrally. Anterior margins flare outward. Tapers sharply at about midway along length of fins where muscular tissue terminates and forms a long tail. Mid antero-ventral margin slightly emarginate between small, sharp lateral angles. Mid antero-dorsal margin produced into a large, broad, blunt angle.

Dermal cushions: Found only on mantle. Evenly spaced, ca. 100–150 μm apart, but sparse on posterior ventral mantle (Fig. 3a). Conical in shape; sharply pointed. Height about 100–200 μm (Fig. 3b). Diameter at base varies from about 50 to 80 μm. Covered with very thin, polygonal plates, possibly epithelial cells; frequently lost at point of cone (Fig. 3c). Interior vacuolated (Fig. 3d). Mantle tissue underneath dermal cushions is slightly vacuolated.

Gladius: Not extracted. Partially visible dorsally through mantle but does not bisect mantle muscle. Forms a ridge along dorsal mantle that turns into a groove between the fins. Visible in tail. Covered by thin, dermal tissue on posterior ventral surface. Length probably about the same as ML.

Fins: Large, rounded, very broad and muscular. Posteriorly concave and extend as fringe on long, slender tail which projects about 16 mm posterior to expanded portion of fins. Anteriorly convex with small lobes. Width is 22.7 mm (41.8% of ML); length is 20.5 mm (37.8% of ML).

Funnel: Short, stout. Not set deeply in funnel groove. Funnel valve large. Funnel organ with large, roughly oval ventral pads, and inverted V-shaped dorsal pad with anterior median papilla and what appear to be broad, low median ridges on the lateral arms.

Funnel-mantle locking cartilage: Straight and simple, very prominent. Funnel element, long with deep, wide median groove. Mantle element, long, thick ridge.

Head: Short; width less than MW, 8.0 mm (14.8% of ML); head length (HL) is 11.8 mm (21.8% of ML). Rounded posteriorly. Eyes occupy about 50% of HL and do not greatly protrude. Eyelids round with pronounced anterior sinus. Posterior, muscular thickening on eyelids and loose, membra-

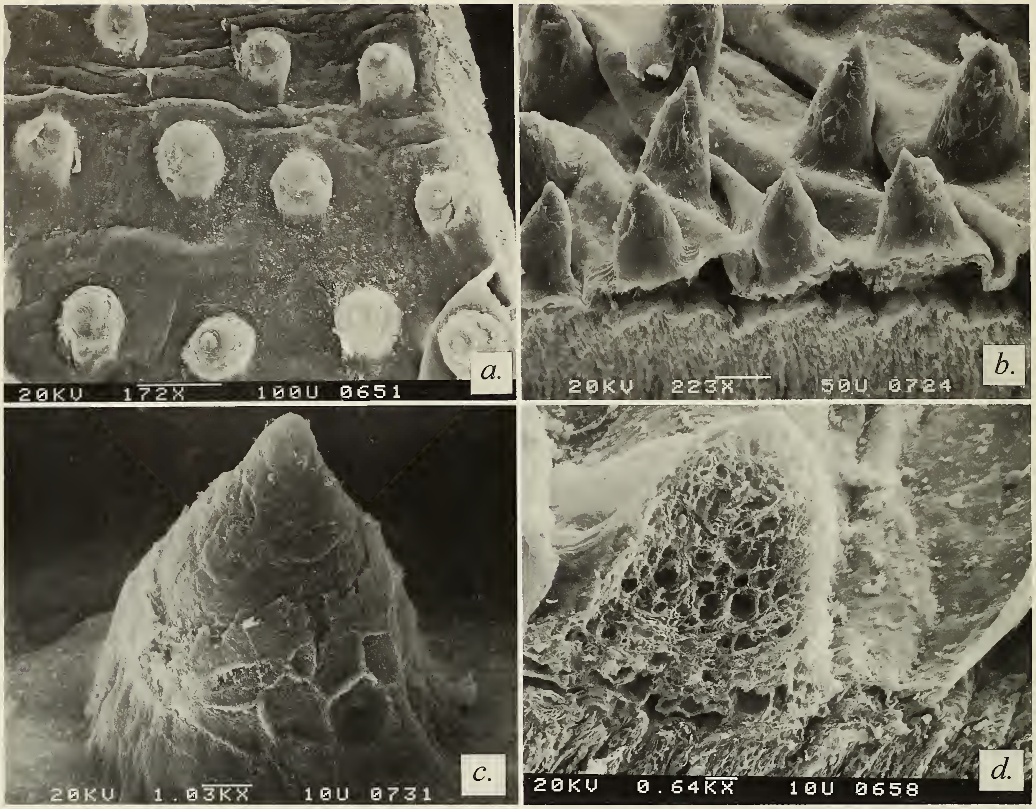

Fig. 3. Dermal cushions from mantle, 54 mm ML: (a) top view, scale: 100 μm (b) lateral view, scale: 50 μm, (c) closeup, scale: 10 μm, and (d) cross section, scale: 10 μm.

nous tissue between eyes and base of arms. One pair of small nuchal folds on either side of funnel groove.

Arms: Long, narrow; attenuate gradually. All keeled for their entire lengths. Arms III most prominently keeled. Arm formula III > II > IV > I on right side but III = II > IV > I on left. Length varies from 23.6 to 29.5 mm (43.5–54.4% of ML). Oral surface with low, trabeculate protective membranes on both margins of all arms. Trabeculae short, narrow and attached to bases of sucker stalks. Suckers biserial, spherical in shape, of approximately uniform size for nearly entire length of all arms. Chitinous sucker rings of proximal suckers with 10–12 large, pointed teeth on distal margins and several very small, rounded teeth on proximal margins. Small distal suckers, with about eight large teeth distally but no teeth proximally.

Tentacles and clubs: Tentacles nearly twice as long as arms; length is 44.1 mm (81.4% of ML). Cross section is elliptical, almost triangular. Club only slightly expanded. Club very long; about 22.5 mm (ca. 51% of tentacle length). Aboral swimming keel originates approximately mid club and extends to distal end. Proximal half of club and stalk with separate, low median aboral keel. Low trabeculate protective membranes equally developed on both margins of clubs proximal of dactylus. Membranes most developed on long manus. Four series of suckers on full length of club; ventral and dorsal pairs of suckers on manus slightly separated by a sucker-free median area (Fig. 2c). Neither suckers or knobs on stalks. Suckers on manus about 350 μm across on longest axis; oval, almost circular, with wide openings (Fig. 4) and not compressed like

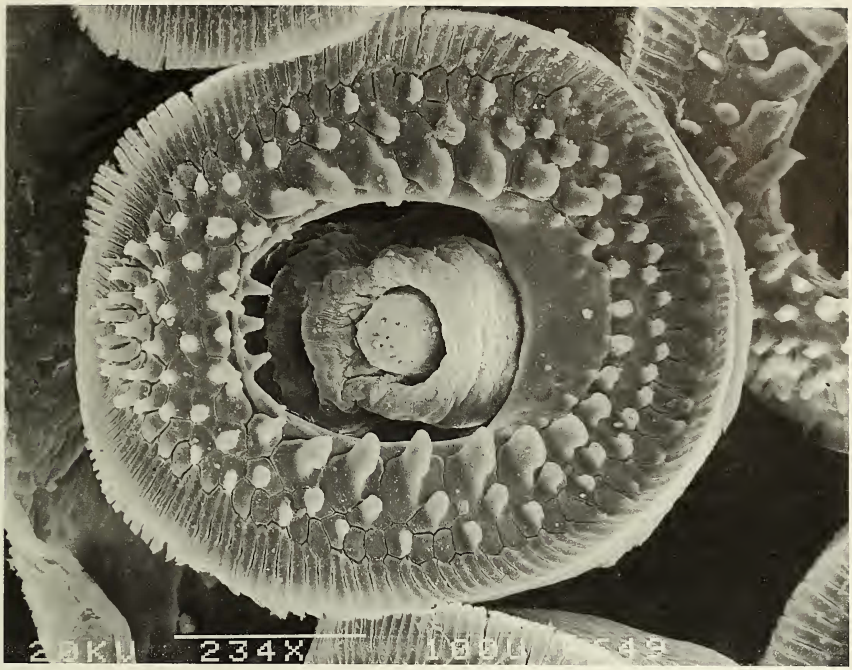

Fig. 4. Mid manal tentacular sucker, 54 mm ML, scale: 100 μm.

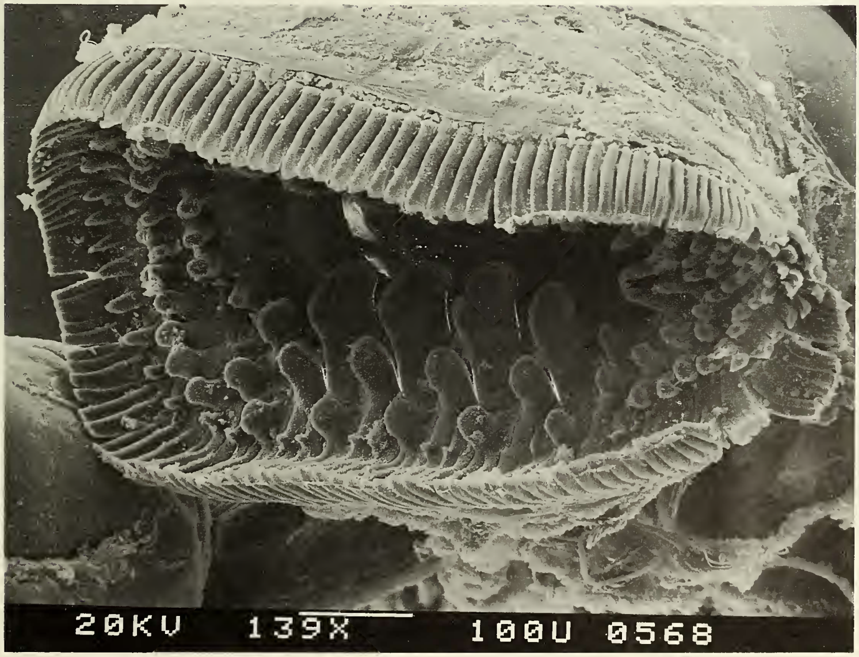

Fig. 5. Mid manal tentacular sucker, 108 mm ML, UMML 31.2369, scale: 100 μm.

suckers in large *P. adami.* Suckers on carpus and dactylus more circular. Suckers on short carpus ca. 80% diameter of those on manus, suckers on moderately short dactylus ca. 60% diameter of those on manus. Peripheral fringe of outer chitinous rings of suckers composed of tooth-like plates; larger, blunt, tooth-like structures present on medial plates with those near interior margins of suckers much larger. Three pronounced teeth on interior distal margins of inner chitinous ring.

Buccal mass: Small; projects outward. Seven large lappets with well-developed connectives attached dorsally to arms I–II, ventrally to arms III–IV. Buccal membrane prominent; translucent but firm. No buccal suckers.

Beak and radula: Not extracted. Protruding rostrums of upper and lower beaks darkly pigmented.

Chromatophores: Present on all parts of specimen; mostly round or oval. Red-brown, mostly flared, vary in intensity from faint to vivid. Numerous and large along dorsal midline of mantle. Large, widely spaced on dorso-lateral and ventral surface of mantle. Form distinct wine-glass pattern on ventral surface. Dense on dorsal surfaces of fins and tail, and ventrally on outer halves of fins; absent on interior halves and ventral surface of tail. Few, mostly contracted, on ventral surface of funnel. Some widely scattered on ventral surface along dorsal margin of funnel groove, midline of head and anterior and posterior to eyes. Few large, irregularly spaced on dorsal surface of head posterior to eyes, and some on posterior and anterior center of head. Two or three indistinct horizontal rows along entire length of arms. Several very small, elongate on distal and proximal edges of suckers. Aboral row along full length of tentacular stalk, dense pattern aborally on club. On oral surface of club, scattered around the bases of the suckers stalks.

Tentacular suckers and dermal cushions of 108 mm and 179 mm ML juveniles.—Tentacular suckers: Mostly oblong and laterally compressed with narrow openings at 108 mm ML, some partially open (Fig. 5). Laterally compressed with narrow openings at 179 mm ML, identical to the condition described for the adult by Voss (1956). Length from about 1000 to 1200 μm at both 108 and 179 mm ML. Tooth-like structures on the infundibulum similar but more robust than at 54 mm ML.

Dermal cushions: Flat-topped and broad, not conical and pointed like in the specimen of 54 mm ML. Positioned relatively much closer, like in adult (Roper & Lu 1990). About 100 μm in height and 300–400 μm across at 108 mm ML; roughly circular or oblong, may have been slightly flattened during handling of specimen; vacuolated (Fig. 6). About 175–250 μm in height and about 500 μm across at 179 mm ML; roughly square or pentagonal; closer together than at 108 mm ML, often touching at the base; vacuolated (Fig. 7). Underlying mantle tissue more highly vacuolated than at 54 mm ML (Figs. 6b, 7b).

Discussion

There are notable differences in some morphological features of the SEFCAR specimen compared with the description and illustration of the later growth stages of *P. adami* in Voss (1956). The size of the specimen illustrated in Voss (1956) is given as 136 mm ML in the figure caption. However, this number is questionable: the mantle lengths of the holotype, paratypes, and additional material listed by Voss were all larger. Nevertheless, differences include the fins, which are shorter and more rounded in the small SEFCAR juvenile compared to larger specimens; the tail, which is longer and narrower in the juvenile; and the tentacular suckers, which are open in the small juvenile and not compressed like those of older individuals. Additionally, the development of the dermal cushions in juvenile *P. adami* with growth consists of a change from widely spaced cones to closely set pen-

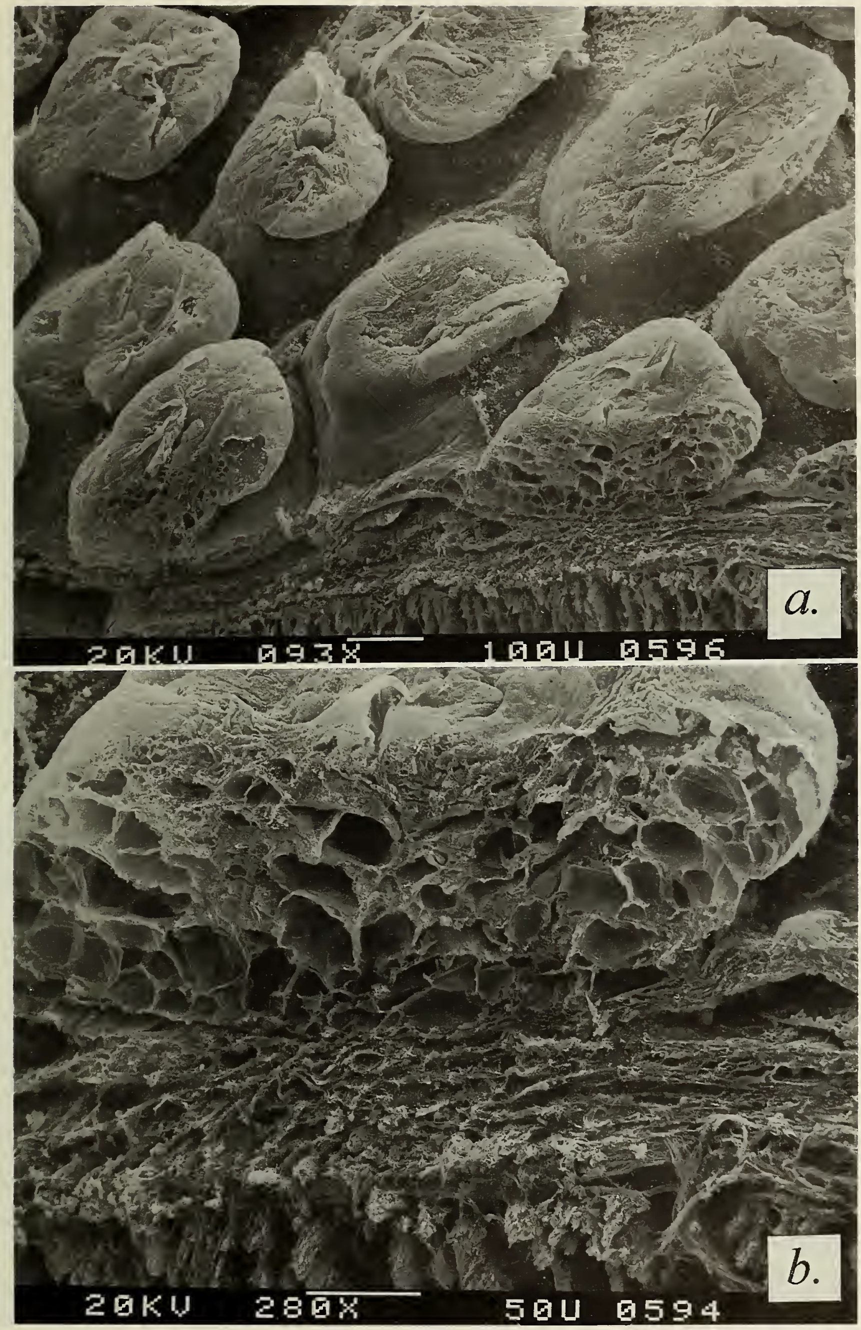

Fig. 6. Dermal cushions from mantle, 108 mm ML: (a) lateral view, scale: 100 μm, and (b) cross section, scale: 50 μm.

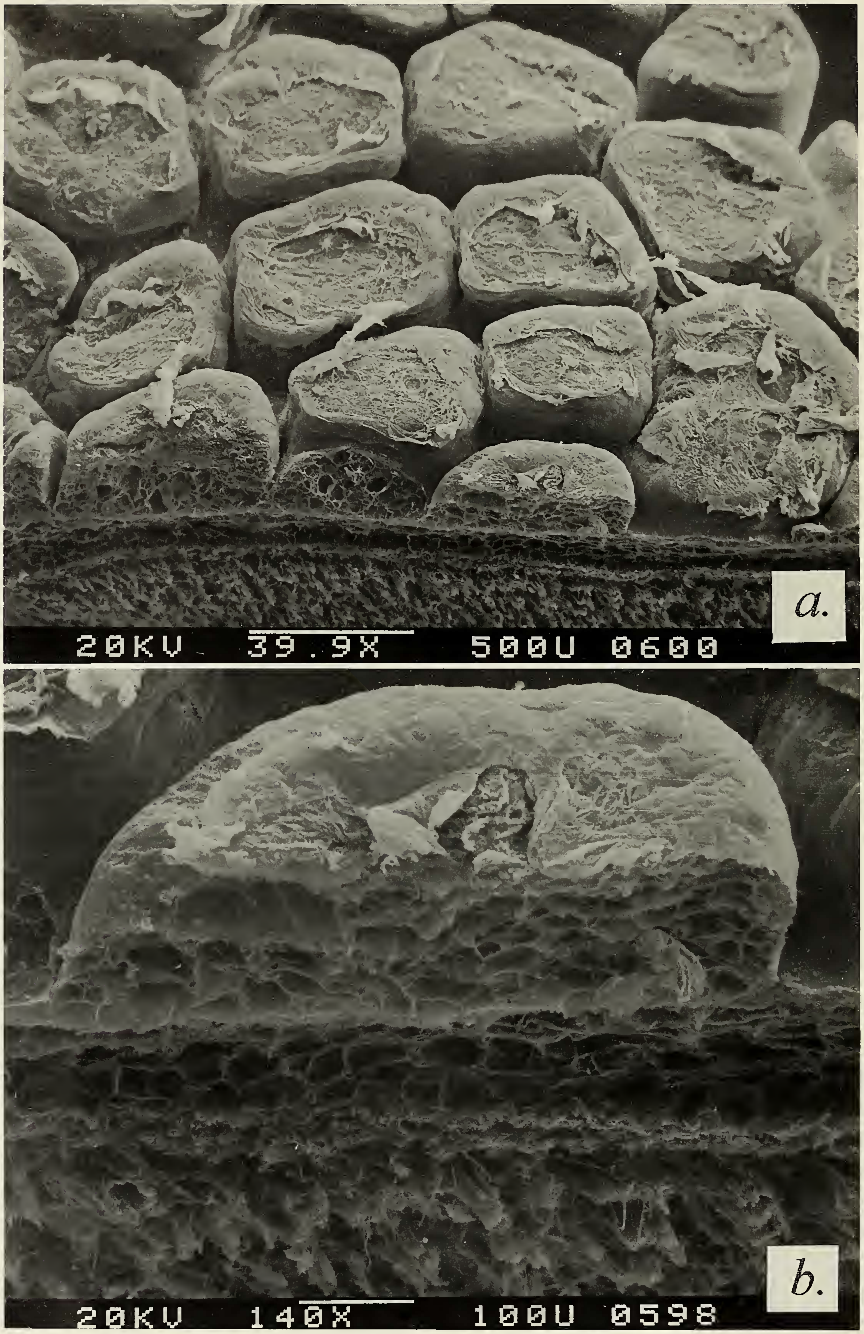

Fig. 7. Dermal cushions from mantle, 179 mm ML, UMML 31.465: (a) lateral view, scale: 500 μm, and (b) cross section, scale: 100 μm.

tagons. The internal structure of the dermal cushions of my *P. adami* juveniles is similar to the vacuolated condition of dermal cushions for the adult described and illustrated by Roper & Lu (1990).

There are also differences in the dermal cushions and tentacular suckers of the SEFCAR specimen compared with the only descriptions of small *Pholidoteuthis* sp.; specimens of 14 mm and 32.8 mm ML in Clarke (1992). Clarke characterized the dermal structures of the specimen of 14 mm ML as the same as those of adults. However, the dermal cushions of the SEFCAR *P. adami* are conical and pointed, so Clarke's 14 mm ML specimen is probably a different species. Furthermore, Clarke stated that the dermal structures of a *Pholidoteuthis* sp. of 32.8 mm ML have small papillae around their margins, similar to the papillose tubercles described by Pfeffer (1912) for the 30 mm ML, juvenile type of *Tetronychoteuthis massyae.* However, there are no marginal papillae on the dermal cushions of the SEFCAR specimen. The papillose tubercles of an immature *T. massyae* of 100 mm ML in Roper & Lu (1990) are similar to the dermal structures of a mature *Pholidoteuthis boschmai* of 286 mm ML in Villanueva & Sanchez (1993), which is in accord with the conclusion of Nesis & Nikitina (1990) that *T. massyae* and *P. boschmai* are conspecific. Therefore, the similarities of the dermal structures of Clarke's 32.8 mm ML *Pholidoteuthis* sp. to the papillose tubercles of *T. massyae* imply that it is *P. boschmai.*

Clarke (1992) described the tentacular suckers of his *Pholidoteuthis* sp. of 14 mm ML as being open and not compressed, and the suckers of his *Pholidoteuthis* sp. of 32.8 mm ML as compressed, the same as in adults. The tentacular suckers of the 54 mm ML SEFCAR specimen, however, are not compressed and are clearly different from those of my older museum juveniles, which have narrow openings like later growth stages of *P. adami* described by Voss (1956). The inconsistency in the size at which compression of the tentacular suckers is present between the specimen at hand and Clarke's specimens is further indication that his specimens are not *P. adami.*

Additionally, the fins in an illustration of Clarke's (1992) specimen of 14 mm ML are proportionally smaller than the SEFCAR juvenile, and the tail is not developed. These and the above incongruities suggest differentiation of Clarke's specimens, at least one of which is likely *P. boschmai,* and my specimen at the generic level. This inference concurs with Toll's (1982) finding that *P. boschmai* and *P. adami* may not be congeneric based on gladius morphology. However, as Roper and Lu (1989) concluded, the status of the type species, *P. boschmai,* must first be resolved before the status of *P. adami* can be revised.

Acknowledgments

I thank N. Voss for reviewing the manuscript and contributing much helpful insight, R. E. Young and an anonymous reviewer for critique that substantially improved the text, C. McSweeny for the illustrations, P. Blackwelder, M. Lynn, and N. Romer for their assistance with the SEM analysis, and M. McGowan for the successful capture of the specimen. This work was supported by National Oceanic and Atmospheric Administration (NOAA) Cooperative Agreements #NA85-WCH-06134 and #NA90RAH00075 to the Cooperative Institute for Marine and Atmospheric Studies (CIMAS), University of Miami. Research operations in the National Marine Sanctuary were conducted under National Marine Sanctuary Permits KLNMS and LKNMS-11-89.

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